Bonobo personality

Bonobo personality: age and sex effects and links with behavior and dominance

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Abstract

The study described in this chapter examines whether individual differences in six rating-based bonobo personality dimensions---Assertiveness, Conscientiousness, Openness, Attentiveness, Agreeableness, and Extraversion---are related to sex and age and behaviors and dominance. To these ends, the study tested predictions based on previous studies of human and chimpanzee personality, and bonobo behavior and socioecology. Sex and age differences in Assertiveness, Openness and Extraversion and correlations between these personality dimensions and behavior were consistent with our predictions. Conscientiousness showed associations with observed behaviors but requires further investigation as sex and age effects differed from those reported in humans and chimpanzees. Agreeableness and Attentiveness showed few associations with age, sex, and behaviors, indicating the need to further investigate validity of these factors. This study shows that personality dimensions in bonobos are correlated with sex, age and behaviors in ways that are consistent with what is known for bonobos and their socioecology.

Keywords: Personality – *Pan paniscus* – Ratings – Codings – Comparative Validity – Construct Validity

Introduction

> "Like other higher primates, pygmy chimpanzees are rich in individuality, and the personality of individuals probably exerts a strong influence on the character of social relationships between group members. […] In the ongoing research then, there is a great need to focus our attention on personality" (Kano, 1992- p.IX)

Bonobos, like all primates, vary in their behavior across individuals (Kano, 1992). While much research focuses on explaining the evolution of species-specific characteristics, only more recently have within-species individual differences become the focus of analysis. Personality is one construct that has been used to describe and explain individual differences within populations. While personality has initially and predominantly been used to help characterize human behavioral diversity, it is now being used to help explain individual differences in animals – including great apes (Gosling, 2001, Mehta and Gosling, 2008). Personality in nonhuman primates and other animals is defined in much the same way as is personality in humans, namely as inter-individual differences in behavior, affect, and cognition that are stable across time and situations (Goldberg, 1990; McCrae & Costa, 1999, Réale et al., 2007). Animal personality has been documented in species ranging from insects to nonhuman primates (Gosling and John, 1999, Carere and Eens, 2005, Gosling, 2001, Freeman and Gosling, 2010), a fact that underlines its importance and early evolution in the animal kingdom.

Most often animal personality is measured using behavioral observations and behavioral tests (Freeman and Gosling, 2010; Staes et al., submitted). However, animal personality is also measured using trait ratings, which involves asking humans familiar with individual animals to rate these animals on a set of predefined traits (Freeman and Gosling, 2010). This approach was at first perceived as 'subjective' and anthropomorphic by behavioral biologists, but very likely reflects real personality constructs so long as they meet the same criteria as behavioral observations and behavioral tests (Gosling and Vazire, 2002, Vazire et al., 2007, Weiss et al., 2012, Baker et al., 2015). The first criterion is that ratings have to be consistent across observers, different times of measurement, and different contexts (Capitanio, 1999, Dutton, 2008, King et al., 2008, Weiss et al., 2011). The second criterion is that the link between personality dimensions and life history parameters, such as sex and age, as well as between personality dimensions and other measures (typically behaviors) has to be established (Capitanio, 1999, Pederson et al., 2005, Uher and Asendorpf, 2008, Murray, 2011, Baker et al., 2015). If males and females face different selection pressures, sex differences in personality may emerge. For example, in many species, males vary more in reproductive success than females, and therefore they may rely more on fitness benefits associated with bolder and more exploratory behavior. In three-spined sticklebacks (*Gasterosteus*

aculeatus) and great tits (*Parus major*), males are bolder than females (van Oers, 2005, King et al., 2013) and risky male behaviors have been shown to increase mating success in guppies (Godin and Dugatkin, 1996).

Factor analytic studies, which seek to uncover latent constructs that make up variation in personality traits, typically yield five broad dimensions---Openness, Conscientiousness, Extraversion, Agreeableness and Neuroticism---collectively known as the Big Five or Five-Factor Model (Goldberg, 1990, McCrae and Costa, 1999). Variations of these dimensions and novel dimensions are found in nonhuman primates, including the great apes (Freeman and Gosling, 2010, Adams et al., 2015). Bonobos are particularly interesting because although they are, together with chimpanzees, the closest living relatives of humans (Prado-Martinez et al., 2013), their social organization and behavior differs from chimpanzees and humans (Boesch et al., 2002, Stumpf, 2007). We therefore expect similar differences to be reflected in their personality. Unfortunately, despite the large number of chimpanzee personality studies, few studies have focused on bonobos, and those that did, involved small sample sizes (Uher and Asendorpf, 2008, Murray, 2011, Garai et al., 2016) or focused on measuring single traits, such as boldness (Herrmann et al., 2011). To complement this existing literature, we obtained personality ratings on154 bonobos. All of the bonobos in our study were rated on the Hominoid Personality Questionnaire (HPQ; Weiss et al., 2015). We found six dimensions (Table 1): bonobo Assertiveness, Openness, and Agreeableness were similar to chimpanzee Dominance, Openness and Agreeableness respectively; Conscientiousness appeared to split into the dimensions Attentiveness and Conscientiousness in bonobos; bonobo Extraversion showed little overlap with its chimpanzee counterpart and we therefore considered it a bonobo-specific factor (Weiss et al., 2015).

Table 1: Comparison of adjectival contents of rated personality dimensions for bonobos and chimpanzees (bonobo data from Weiss et al. 2015, chimpanzee data from Weiss et al. 2007; Weiss et al. 2009)

Bonobo		Chimpanzee	
Dimension	**Adjectives**	**Dimension**	**Adjectives**
Assertiveness	**+ Independent** **+ Dominant + Decisive** **+ Persistent** + Cool + Stable - Excitable **- Dependent – Submissive** **- Timid** - **Vulnerable** **- Anxious** - Fearful	Dominance	**+ Independent** **+ Dominant + Decisive** **+ Persistent** + Stingy + Manipulative - **Dependent - Submissive** **- Timid - Vulnerable** **- Anxious**
Conscientious-ness	+ Gentle + Predictable **- Impulsive - Defiant** **- Reckless - Irritable** **- Aggressive – Jealous** **- Bullying –** Manipulative - Erratic - Stingy	Conscientious-ness	**- Impulsive - Defiant** **- Reckless - Irritable** **- Aggressive - Jealous** **- Bullying** – Disorganized - Excitable - Clumsy - Unperceptive - Distractible - Thoughtless
Openness	**+ Inquisitive + Inventive** **+ Innovative + Curious** + Active + Playful + Imitative - Lazy - Conventional	Openness	**+ Inventive + Inquisitive** **+ Innovative + Curious** + Cautious
Attentiveness	**+ Intelligent** – Clumsy - Unperceptive - Distractible - Thoughtless - Disorganized	Neuroticism	**+ Intelligent** + Erratic +Depressed + Fearful + Autistic - Stable -Unemotional - Cool
Agreeableness	**+ Friendly + Affectionate** **+ Protective** **+ Sympathetic + Helpful** **+ Sensitive** + Sociable	Agreeableness	**+ Friendly + Affectionate** **+ Protective + Sympathetic + Helpful + Sensitive** + Gentle + Conventional
Extraversion	**- Individualistic – Solitary** - Autistic - Depressed	Extraversion	+ Active + Playful + Sociable **- Individualistic – Solitary** - Lazy

Boldface indicates that variables are similar in these dimensions for both species

Based on what is known about human and chimpanzee personality, and about the ecology and social structure of bonobos, we made several predictions about sex and age differences in bonobo personality. We then tested these predictions, that is, we examined the 'comparative validity' of the dimensions found in our previous study (Weiss et al., 2015). In terms of sex differences, among chimpanzees, males consistently score higher than females on Dominance, which has high loadings of traits, such as *dominant*, *independent*, and *bullying* (Weiss et al., 2007, King et al., 2008, Weiss and King, 2015). Also, compared to females, male chimpanzees score lower on Conscientiousness, which has high negative loadings on traits, such as *aggressive* and *impulsive* (Weiss *et al.* 2007; King *et al.* 2008; Weiss & King 2015). Compared to the male dominated societies in chimpanzees (Boesch and Boesch-Acherman, 2000, Goodall, 1986), in bonobo societies females dominate males, but not all females are

higher ranking than all males, a condition known as "partial female dominance" (Furuichi, 2011, Vervaecke et al., 2000a, Stevens et al., 2007, Surbeck and Hohmann, 2013). We therefore expect sex differences in bonobos to be the opposite of those found in chimpanzees for these two factors. In other words, we expected that bonobo females will score higher on Assertiveness and lower on Conscientiousness than male bonobos.

Personality is also known to show moderate developmental changes. For example, cross-sectional and longitudinal studies in humans show that Agreeableness and Conscientiousness increase with age, while Extraversion and Neuroticism decrease, and Openness increases and then later decreases (McCrae et al., 1999, McCrae et al., 2000, Costa et al., 2001). Age differences in chimpanzee personality describe similar trends. Older chimpanzees score higher in Dominance, Conscientiousness, and Agreeableness, and lower in Extraversion and Openness than younger individuals (King et al., 2008, Weiss and King, 2015, Dutton, 2008). These patterns, therefore, appear to be conserved across chimpanzees and humans. We thus expect that, compared to younger bonobos, older bonobos will score higher on Assertiveness and Agreeableness, and lower on Openness. On the other hand, it has been suggested that bonobos retain juvenile characteristics into adulthood, including high levels of social tolerance, play and nonconceptive sexual behavior (Hare et al., 2012; Wobber et al., 2010). If this is the case, age effects for dimensions that are associated with these behaviors may be less pronounced in bonobos. As the remaining 3 bonobo dimensions, Attentiveness, Conscientiousness and Extraversion, differ structurally from the human and chimpanzee dimensions, it is difficult to predict age effects for these dimensions based on our knowledge from human and chimpanzee personality. We will therefore explore differences in these dimensions as a basis for future studies. .

In addition to testing comparative validity by examining sex and age differences in personality, it is important to test for construct validity of the dimensions, by looking at how personality correlates with other measures in ways that are consistent with the meaning (and likely function) of these dimensions (Capitanio, 1999, Paunonen, 2003, Pederson et al., 2005, Uher and Asendorpf, 2008, Murray, 2011, Baker et al., 2015). One way to assess the construct validity of these ratings-based measures is to examine their correlations with naturally occurring behaviors (Pederson et al., 2005, Vazire et al., 2007, Konečná et al., 2008, Uher and Asendorpf, 2008) and/or behaviors in response to experimental tests (Baker et al., 2015, Carter et al., 2012). In behavioral tests stimuli are introduced to provoke behaviors that occur infrequently or that are difficult to observe in a naturalistic context. For example, novel food/object tests or predator experiments have been used to assess novelty seeking and boldness in several species (Carere and Eens, 2005, Carter et al., 2012, Massen et al., 2013, Andersson et al., 2014, Baker et al., 2015).

Previous studies of the construct validity of animal personality have shown that the time it took for common squirrel monkeys (*Saimiri sciureus*) to approach novel objects was negatively associated with their scores on Sociability and that the time it took black crested macaques (*Macaca nigra*) to touch novel objects was negatively associated with Dominance (Baker et al., 2015). Studies looking at the associations between personality traits and behaviors have been conducted in bonobos, but understandably these studies only involved five and four individuals, respectively (Uher and Asendorpf, 2008, Murray, 2011). The present study includes a larger number of individual bonobos, and thus benefits from greater statistical power. In chimpanzees, associations have been found for several factors and variables (Pederson et al., 2005, Vazire et al., 2007, Murray, 2011). For example Dominance is positively correlated with aggression given and negatively correlated with submissive behaviors; Extraversion is positively correlated with social and affinitive behaviors; and Sociability is positively correlated with play (Murray, 2011, Pederson et al., 2005, Vazire et al., 2007, Buirski et al., 1978). Based on the findings in chimpanzees, we expect to find similar associations in bonobos. For example, bonobo Assertiveness should correlate positively with aggression and dominance rank and negatively with submissive behaviors. We expect Extraversion to correlate positively with social and affinitive behaviors like grooming, play and sexual interactions. Lastly, we expect Openness to correlate positively with exploratory behaviors, like approaching new stimuli. Finally, to rule out that raters rate the individuals based on their own stereotypical beliefs about age, sex and social position of human individuals, we also test for sex and age differences in the observed behavioral variables. If age and sex effects are found for rated dimensions, they should show similar effects in the behavioral variables that are correlated with the rated personality dimensions.

In summary, this study will 1) assess the comparative validity of bonobo personality dimensions, by testing whether sex and age differences in personality are consistent with what we would expect based on findings related to these differences in chimpanzees and humans and with differences between bonobos and chimpanzees in social structure, behavior and life history; 2) test construct validity of the dimensions, by examining their associations with relevant behavioral variables derived from naturalistic observations and behavioral tests. We first test for age and sex effects of these behavioral variables and then look for associations between personality dimensions and behavioral variables. Based on studies done in multiple other species, we predict that the bonobo personality dimensions will show appropriate associations with observed behaviors.

Methods

Questionnaire ratings

Personality ratings were independently collected by different raters for 154 bonobos (71 males, 83 females) with ages ranging from 2 to 62 years using the Hominoid Personality Questionnaire (Weiss et al., 2009) in two waves (first wave 2006-2008, second wave 2012) (See Weiss *et al.* 2015 for details). The interrater reliabilities and repeatabilities of the six dimensions revealed by these ratings were high enough to justify their being used in further studies.

Naturalistic observations

For 44 individuals (18 males and 26 females) that were rated, behavioral data were collected by researchers (NS and 8 students she supervised) who did not rate the bonobos on the HPQ. Each student received at least three weeks of training. After each student was trained, their inter-observer reliability was tested by scoring two 10-minute bonobo focal video recordings. High Spearman rank correlations (mean r=0.86) were found across all observers coding the behaviors (Martin and Bateson, 1993). Observations involved alternating continuous 10 minute focal observations, with instantaneous group scan sampling. During focal observations the main activity of the focal individual was recorded. All self-directed behaviors and social interactions were also recorded. Scans were used to determine spatial proximity measures for all individuals in the group in between each focal observation. During the entire observation period, bouts of agonistic behavior were recorded using all occurrence sampling. In total, 1666.15 hours of focal observations (mean 32.04 hours per individual), 10 472 group scans (mean 616 per individual) and 2132 hours of all occurrence sampling of aggression (mean 39.5 hours per individual) were collected. Behavioral observations were coded using the Observer (Noldus version XT 10, the Netherlands).

Variables based on durations of behavioral states (activity, grooming given, grooming received, individual play, social play, auto-scratching, and auto-grooming) were calculated as the proportion of individual focal time performing the behavior. Behavioral variables based on occurrences of events (submission, aggression given, aggression received, socio-sexual behaviors) were calculated as frequencies per hour, corrected for individual total observation times (both focal observation times and all occurrence observation times). Sit alone was calculated as

the proportion of all scans where the subject was recorded as being alone with no other individuals sitting within a 2m radius. Number of neighbors was the average number of neighbors present in scans where the subject was recorded as being in proximity (within 2m) of at least one other group member. Grooming density given and received was calculated as the proportion of available grooming partners that were groomed by the subject or who groomed the subject. Grooming diversity was calculated with the Shannon-Wiener index (Di Bitetti, 2000), corrected for group size effects as follows:

$$\text{Grooming diversity} = H/H_{max}$$

$$H = -\Sigma(p_i \times \ln(p_i))$$

in which p_i is the proportion of the individual's grooming effort given to the ith individual

$$H_{max} = \ln(N - 1)$$

in which N is the number of individuals in the group. Grooming diversity results are in a value between 0 and 1, with 0 meaning perfect skew with all grooming directed to one individual, and 1 meaning perfect equality, i.e., all grooming partners receive an equal amount of grooming.

Dominance rank was measured by assigning normalized David's scores to each individual, based on the occurrence of fleeing upon aggression (de Vries et al., 2006, Stevens et al., 2007). David's scores use dyadic dominance proportions to calculate cardinal ranks for each individual based on the proportions of wins and losses in agonistic encounters. An individual loses an agonistic interaction when it flees as a response to the aggression. We then standardized the David's scores by dividing them by group size to test overall associations of rank with personality traits.

Behavioral experiments

We conducted eight group experiments (Figure 1), adapted from previous work on chimpanzees (Massen et al., 2013). In the predator experiments, two model predators were used: a taxidermied leopard in crouching position with bared teeth and a 4m long snake made out of a fire hose and clay, and painted to resemble a python. As leopards are natural predators of bonobos in the wild (D'Amour et al., 2006) and pythons are assumed to be natural predators of bonobos in the wild (Kano, 1992), these model predators should be representative of threats that wild bonobos would face. Both models were placed in sight, but out of reach of the bonobos and the bonobos' behavior towards the models was scored. These behaviors included number of approaches, time spent in proximity, and the number of displays against the mesh, including both poking with sticks and banging the mesh,

behind which the predator was placed. The snake experiment was dropped from further analysis as the bonobos did not respond to the model python and subsequently, there was little variation in response.

In two novel food experiments, bonobos were given durian fruit and pasta, the latter being dyed blue with an edible dye. During the durian fruit experiment, two fruits were placed in the enclosure a few meters apart to avoid their being monopolized by one individual. Two cameras were used to track both fruits at the same time. During the pasta experiment, 250g of pasta were boiled, left to cool and then put in two piles in the enclosure, again, some meters apart to avoid their being monopolized by one individual. In these experiments we measured latency to approach the food closer than 2m (in seconds) and whether the subject tasted the food item (0 = no, 1 = yes). When an individual did not approach the food item, it was given the maximum duration of 1800s.

In each of four puzzle feeder experiments, bonobos were given a different foraging device. The first was a hanging barrel filled with seeds ("Hanging Barrel"). The second was a barrel filled with water and pieces of pear that sank to the bottom. This barrel was covered on top with a square mesh that was too small for an adult bonobo's hand to fit through ("Barrel with Mesh"). As sticks were needed to get to the pear in the "Barrel with Mesh" condition, we measured the proportion of time during which subjects used sticks. The third puzzle feeder was a seed-filled hanging double tube system that had to be rotated for it to release its contents ("Tubes"). The final puzzle feeder ("Reel and Feed") was a crate hanging from the outside of a mesh door next to the enclosure. To obtain the fruit and/or vegetables in this crate, bonobos had to tilt the crate using a rope that was hanging in the enclosure. For all puzzle feeders the following behavioral variables were measured: the time in seconds to approach the puzzle within 2m, the proportion of time spent manipulating the puzzle, the proportion of time spent within 2m of the puzzle without touching it, the number of times the puzzle was approached.

All behavioral experiments were filmed (Canon Legria FS406, Japan) and recordings were coded using Observer Video-Pro (Noldus version XT 10, the Netherlands). Data recording started as soon as the group had access to the stimuli and was stopped after 30 minutes. All group members had access to the stimuli at the same time. In four out of six groups (FR, TW, ST, AP), group compositions differed between testing due to artificial fission-fusion of groups by zoo management. The order of the experiments was randomized and there were at least 3 days between experiments.

Figure 1. Behavioral variables from eight experiments were collected to assess their association with rated personality traits. Bonobos were tested in three different experimental contexts: Predator experiments included a fake python (1) and taxidermied leopard (2). Puzzle feeder experiments included turning tubes puzzle (3), reel and feed puzzle (4), Barrel with mesh puzzle (5) and hanging barrel puzzle (6). Novel food experiments included blue dyed pasta (7) and durian fruit (8).

Analyses

Sex, age and rank differences in rated dimensions

To test whether personality dimensions were associated with sex, age, or dominance rank, we used linear mixed models using the lme4 package (Bates et al., 2015) in R (www.r-project.org, version 3.1.0). In each model, sex, age, and dominance rank were entered as fixed effects and group was entered as a random intercept to account for non-independence of observations within the same zoo. To test for the significance of the fixed effects we used F-tests with a Kenward-Roger correction for the number of degrees of freedom. The corrected F-tests were computed using the pbkrtest package (Halekoh and Hojsgaard, 2014). Inspection of residual plots did not reveal obvious deviations from homoscedasticity or normality.

Sex and age effects in behavioral variables

Independent-samples t-tests and Pearson correlations were used to test for sex and age differences, respectively, in the behavioral variables. We inspected qq-plots and plots of residuals against fitted values to check whether the assumptions of normally distributed and homogeneous error variance were fulfilled. These did not indicate severe violations of these two assumptions. As few personality studies apply a correction for multiple testing, and a Bonferroni correction in behavioral ecology may be overly conservative (Nakagawa, 2004), we reported results with and without Bonferroni correction.

Construct validity

These analyses were restricted to the 44 individuals (18 males and 26 females) for whom ratings and behavioral observations data were available. As the behavioral observations were made between 2011 and 2014, we only used ratings collected during the second wave in 2012. We used Spearman rank correlation coefficients to assess the association between the personality factors and the behavioral variables. Again, we reported results with and without Bonferroni correction.

Ethics

The study was approved by the Scientific Advisory Board of the Royal Zoological Society of Antwerp and the University of Antwerp (Belgium) and endorsed by the European Breeding Program for bonobos. All research complied with the ASAB (2012) guidelines.

Results

Relation of age, sex and rank with personality dimensions

Male bonobos scored significantly lower than females on Assertiveness, *b*=-0.939, s.e.=0.185, F(1,104)=25.48, p<0.001, and Extraversion, *b*=-0.612, s.e.=0.161, F(1,103)=14.28, p<0.001 (Figure 2). A significant association with age was found for Openness, *b*=-0.052, s.e.=0.006, F(1,106)=70.54, p<0.001, and Extraversion, *b*=-0.017, s.e.=0.007, F(1,106)=5.64, p=0.019, with older individuals scoring lower on both dimensions (Figure 3). The other dimensions did not differ significantly by sex, Conscientiousness: *b*=0.299, s.e.=0.191, F(1,108)=2.38, p=0.126; Openness: *b*=-0.155, s.e.=0.140, F(1,101)=1.20, p=0.274; Agreeableness: *b*=-0.241, s.e.=0.149, F(1,98)=2.60, p=0.110; Attentiveness: *b*=-0.139, s.e.=0.149, F(1,102)=0.87, p=0.355, or by age, Assertiveness: *b*=-0.006, s.e.=0.008, F(1,106)=0.64, p=0.425; Conscientiousness: *b*=0.008, s.e.=0.008, F(1,109)=0.97, p=0.326; Agreeableness: *b*=0.011, s.e.=0.007, F(1,101)=2.75, p=0.100; Attentiveness: *b*=-0.006, s.e.=0.007, F(1,105)=0.74, p=0.392.

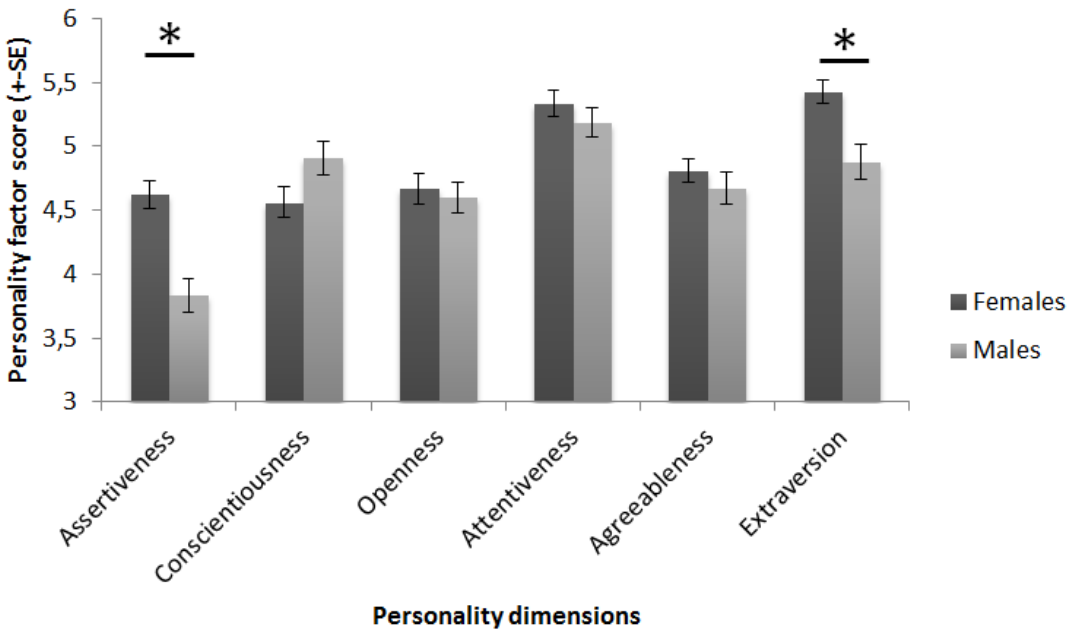

Figure 2. Sex difference in mean scores on personality dimensions (± standard error). Significant effects were found for Assertiveness and Extraversion with females scoring higher than males on both factors. The other dimensions showed no significant sex difference.

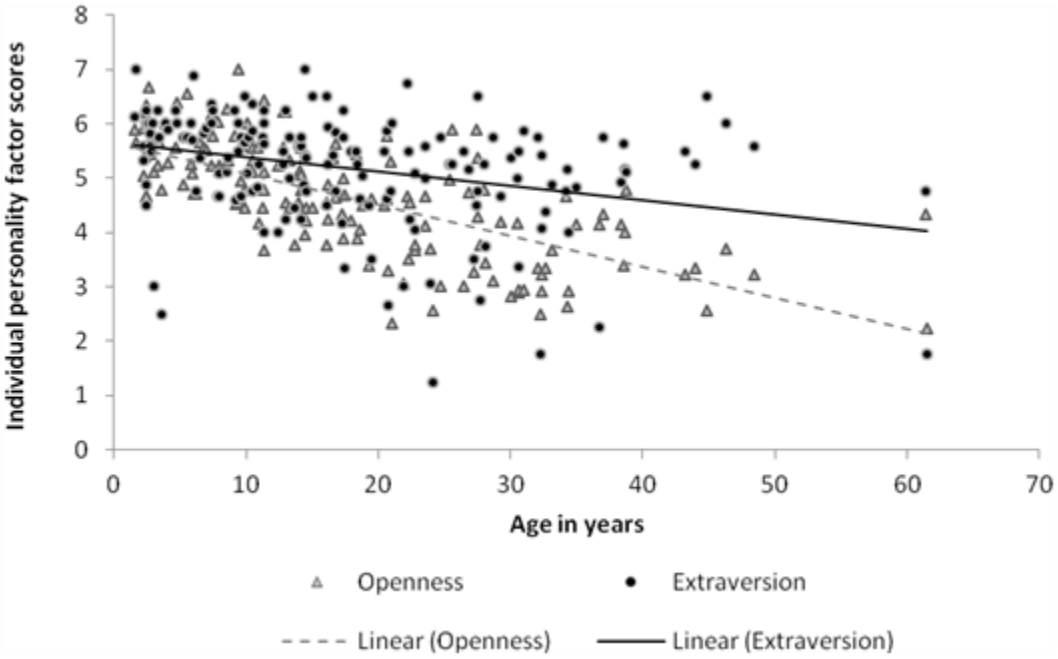

Figure 3. Correlation between age and individual personality factor scores for Openness and Extraversion. The other dimensions showed no significant sex difference.

Sex and age differences in behavior

Tests for sex and age differences in the behavioral variables (Table 2) revealed that, after Bonferroni correction, females scored significantly higher than males on number of neighbors sitting in proximity and time spent time in proximity to the leopard and puzzles. Males scored significantly higher than females on levels of aggression received and frequency of fleeing upon aggression. Older individuals scored significantly lower on the number of times they approached the puzzle feeders.

Table 2: Sex and age differences for observed behavioral variables

	Sex							Age	
	B	**se**	***t***	**df**	***p***	**95% CI**		***r***	***p***
						Lower	Upper		
Grooming Given	0.207	0.203	1.02	42	0.314	-0.203	0.617	-0.289	0.057
Grooming Received	**0.401**	**0.173**	**2.32**	**42**	**0.026**	**0.051**	**0.751**	-0.068	0.659
Grooming Density Given	0.025	0.075	0.33	42	0.746	-0.128	0.177	**-0.369**	**0.014**
Grooming Density Received	0.063	0.073	0.85	42	0.399	-0.086	0.211	0.006	0.970
Grooming Diversity index	0.020	0.072	0.28	42	0.784	-0.125	0.165	-0.168	0.276
N. of Neighbors	**0.193***	**0.051**	**3.78**	**42**	**<0.001**	**0.090**	**0.296**	-0.098	0.526
Be Approached	**1.606**	**0.500**	**3.21**	**42**	**0.003**	**0.598**	**2.615**	0.014	0.927
Approach	-0.373	0.684	-0.55	42	0.589	-1.754	1.008	**-0.444**	**0.003**
Play	-0.112	0.681	-0.16	42	0.870	-1.486	1.262	-0.259	0.090
Point Affinitive	-0.147	0.143	-1.03	20	0.317	-0.446	0.152	**-0.364**	**0.015**
Sexual interactions	0.300	0.199	1.51	42	0.139	-0.101	0.701	**-0.311**	**0.040**
Activity	-0.014	0.034	-0.41	42	0.686	-0.083	0.055	-0.295	0.052
Aggression Given	0.011	0.024	0.45	42	0.653	-0.038	0.060	-0.159	0.302
Aggression Received	**-0.277***	**0.075**	**-3.68**	**42**	**<0.001**	**-0.428**	**-0.125**	**-0.327**	**0.031**
Flee upon aggression	**-0.670***	**0.160**	**-4.19**	**29**	**<0.001**	**-0.996**	**-0.343**	-0.148	0.337
Autogroom	-0.126	0.397	-0.32	42	0.753	-0.926	0.675	-0.026	0.864
Nosewipe	-0.355	1.179	-0.30	42	0.765	-2.734	2.023	0.012	0.936
Scratch	1.666	0.964	1.73	42	0.091	-0.280	3.612	0.140	0.364
Leopard Latency	-61.681	75.260	-0.82	42	0.417	-213.562	90.201	**0.300**	**0.048**
Leopard Proximity	**18.413***	**4.946**	**3.72**	**39**	**<0.001**	**8.407**	**28.419**	0.186	0.226
Leopard N. of Approaches	-0.001	0.001	-0.57	42	0.573	-0.002	0.001	**-0.375**	**0.012**
Leopard N. of Displays	0.001	0.001	1.25	42	0.219	0.000	0.001	-0.244	0.110
Novel Food Latency	-120.941	76.908	-1.57	26	0.128	-279.150	37.268	0.192	0.211
Novel Food Taste	0.038	0.074	0.52	42	0.607	-0.111	0.188	**-0.402**	**0.007**
Puzzle N. of Approaches	0.001	0.001	1.12	42	0.270	-0.001	0.002	**-0.553***	**0.001**
Puzzle Time Manipulated	**11.555**	**3.821**	**3.02**	**30**	**0.005**	**3.750**	**19.361**	-0.181	0.239
Puzzle Proximity	**8.956**	**4.415**	**2.03**	**42**	**0.049**	**0.046**	**17.867**	**-0.402**	**0.007**
Puzzle Latency	**-304.673**	**115.380**	**-2.64**	**21**	**0.015**	**-544.905**	**-64.441**	0.278	0.068
Puzzle Tool Use	4.894	8.090	0.60	42	0.548	-11.432	21.219	-0.078	0.613

Boldface indicates p<0.05, *Significant after Bonferroni correction (p<0.001), N=44

Personality dimensions and behavioral variables

Correlations between personality dimensions based on ratings and behaviors are shown in Table 3. The correlations that survived Bonferroni correction indicated that individuals that score higher on Assertiveness received more grooming, less aggression and showed fewer fleeing upon aggression. Likewise, individuals scoring low on Conscientiousness showed higher frequencies of grooming interactions and individuals scoring high on Openness showed higher levels of approaching behavior towards puzzles and leopard and were more inclined to taste novel food. Agreeableness, Extraversion and Attentiveness were not significantly correlated with the behavioral variables after correction for multiple tests.

Table 3: Spearman rank-order correlations between personality factors derived from HPQ and behavioral variables

		Assertiveness	Consientiousness	Openness	Agreeableness	Extraversion	Attentiveness
Observations	Grooming Given	0.21	**-0.50***	0.26	-0.02	**0.31**	0.27
	Grooming Received	**0.43***	**-0.50***	0.15	0.07	**0.31**	0.15
	Grooming Density Given	0.01	**-0.33**	**0.42**	0.01	0.19	0.17
	Grooming Density Received	0.13	-0.29	0.04	0.07	0.03	0.16
	Grooming Diversity index	0.01	-0.26	**0.34**	0.06	0.09	0.24
	N. of Neighbours	**0.31**	**-0.30**	0.12	0.19	0.26	0.13
	Be Approached	**0.32**	-0.04	-0.12	0.21	**0.31**	0.08
	Approach	-0.04	-0.23	**0.44**	-0.07	0.18	0.12
	Play	-0.04	-0.04	**0.32**	-0.14	0.26	-0.03
	Point Affinitive	-0.11	**-0.38**	**0.40**	-0.03	0.18	-0.01
	Sexual interactions	0.07	**-0.42**	**0.44**	0.02	**0.30**	-0.07
	Activity	0.02	**-0.39**	**0.51**	-0.13	0.19	0.12
	Aggression Given	-0.09	**-0.34**	0.16	-0.12	0.04	0.02
	Aggression Received	**-0.39***	0.19	0.18	**-0.43**	-0.16	0.01
	Flee upon aggression	**-0.57***	0.24	0.11	-0.20	-0.14	-0.06
	Dominance	0.29	**-0.34**	0.06	0.15	0.12	0.02
	Autogroom	-0.04	-0.13	-0.08	-0.27	-0.14	-0.17
	Nosewipe	-0.17	0.04	-0.04	0.14	-0.05	0.18
	Scratch	0.01	0.21	-0.12	0.09	-0.01	0.03
Predator test	Leopard Latency	-0.02	0.11	**-0.40**	0.06	**-0.30**	0.02
	Leopard Proximity	0.27	-0.14	**0.34**	0.26	0.13	0.12
	Leopard N. of Approaches	-0.10	-0.24	**0.47***	-0.02	0.06	0.05
	Leopard N. of Displays	0.08	-0.29	0.29	-0.06	0.07	0.12
Novel food test	Novel Food Latency	-0.18	**0.37**	**-0.37**	-0.05	**-0.41**	-0.11
	Novel Food Taste	-0.16	**-0.38**	**0.50***	0.03	0.15	-0.01
Puzzle feeder tests	Puzzle N. of Approaches	-0.05	**-0.37**	**0.54***	-0.06	**0.40**	-0.03
	Puzzle Time Manipulated	**0.34**	-0.29	**0.30**	0.13	**0.38**	0.19
	Puzzle Proximity	-0.06	-0.27	**0.31**	-0.06	**0.31**	-0.06
	Puzzle Latency	-0.24	**0.45**	**-0.38**	-0.02	**-0.41**	-0.10
	Puzzle Tool Use	0.20	-0.15	0.27	0.19	**0.31**	0.15

Correlations in boldface are significant ($p<0.05$). *Significant after Bonferroni correction ($p<0.001$), N=44

Discussion

We tested whether bonobo personality dimensions derived by ratings demonstrated comparative validity by testing whether sex and age differences were consistent with what we would expect based on findings related to these differences in chimpanzees and humans and with differences between bonobos and chimpanzees in social structure, behavior and life history. We also tested whether these dimensions demonstrated construct validity by examining their associations with behavioral variables derived from naturalistic observations and behavioral tests. The Assertiveness, Openness, and Extraversion dimensions showed good comparative and construct validity. Conscientiousness showed evidence for construct validity but not comparative validity. Agreeableness and Attentiveness did not show evidence for comparative or construct validity in this study.

Previous studies that used different questionnaires and/or behavioral measures also reported modest to strong validity coefficients in apes (see Murray 2011). Many of the associations found in this study, did not reach the $p<0.001$ required by the Bonferroni correction, which is not surprising given the relatively small sample size in this study compared to similar studies of humans (Paunonen, 2003). Although a larger sample size would have increased our power to detect associations between personality dimensions and behaviors, the sample size in this study was already relatively large for a study done in great apes and increasing it further was not possible due to time constraints. Moreover, it should be borne in mind that Bonferroni correction might be considered overly conservative, especially given the modest effect sizes common in the field of behavioral ecology research (Nakagawa, 2004). Despite the correlations not being significant after correction, many of the observed behaviors actually showed associations that were in line with our predictions.

Assertiveness was associated with variables related to social attractiveness in bonobos. This is consistent with studies that show that high ranking bonobos are groomed more often (Franz, 1999, Vervaecke et al., 2000b) and are less likely to be the targets of aggression (Paoli and Palagi, 2009). Studies in other nonhuman primates found similar results for similar personality dimensions. For example, in chimpanzees (Murray, 2011) and rhesus macaques (Capitanio, 1999), a personality dimension labeled Confidence was associated with receiving more grooming. Moreover, in gorillas (Kuhar et al., 2006) and chimpanzees (Pederson et al., 2005), personality dimensions labeled Dominance were negatively related to showing submissive behavior and positively related to receiving submissive behavior.

In line with our expectations, differences in personality between male and female bonobos were largely the opposite as what has been found in chimpanzees (King et al., 2008). For one, females scored higher on

Assertiveness than males. This is consistent with the bonobo's social system, where females occupy the higher ranks in the dominance hierarchy (Vervaecke et al., 2000a, Furuichi, 2011). It is also consistent with findings in hyena, another species in which the females are dominant, where females scored higher on Assertiveness than males (Gosling, 1998). This sex difference in Assertiveness was further supported by our finding of similar sex differences in behaviors: females were groomed more often, received less aggression, and displayed submissive behaviors less often than did males.

Openness was associated with variables that reflect curiosity and play, two facets of Openness that have been identified across many species (Gosling and John, 1999). Further supporting the comparative validity of the dimension, as in humans and chimpanzees (Costa et al., 2001, Mc Crae et al., 2000, King et al., 2008, Weiss and King, 2015), Openness and behavioral variables related to Openness, for example, exploring puzzles, novel foods, and leopards were lower in older individuals. As Openness showed the strongest positive associations with behaviors related to play, and affinitive and sexual interactions, the decline of Openness with age suggests that there is no support in this study for the hypothesis that the retention of juvenile levels of these traits in adult bonobos may be causing less pronounced age-related effects on personality. Similar age related effects were found for Extraversion, a dimension that was positively associated with variables related to social integration, which was in line with our prediction that age effects are stable across closely related primate species. However, none of the associations reached the $p<0.001$ significance level.

In contrast to the lack of sex differences in extraversion among chimpanzees (King et al., 2008, Weiss and King, 2015), female bonobos were significantly more extraverted than males. However, this could be due to the fact that the traits associated with Extraversion differed between bonobos and chimpanzees. Specifically, unlike chimpanzees, for whom Extraversion is defined by traits related to gregariousness, activity, and affect (Weiss et al., 2009, Weiss and King, 2015, Weiss et al., 2007, Weiss et al., 2015, King et al., 2008), the bonobo variant of Extraversion is defined by only a few traits related to social integration and affect (Weiss et al., 2015). Nonetheless, the sex differences in bonobos are consistent with the strength of social relationships in male and female bonobos, where male social bonds are relatively weak while relationships among females and between females and their adult sons are strong (Kano, 1992, Parish, 1996, Hohmann and Fruth, 2002, Stumpf, 2007, Stevens et al., 2015). One previous study reported that bonobo males behaved more extraverted than females (Schroepfer-Walker et al., 2015), however, the behavior recorded in this study was directed towards a human experimenter and not conspecifics. Furthermore, behavior towards caretakers or experimenters was not included in our study. As chimpanzees who are more extraverted attend more often to other chimpanzees than to humans(Pederson et al., 2005), and chimpanzees that had high levels of early human exposure scored lower on Extraversion (Freeman et

al., 2016), these seemingly contradictory findings may, in fact, be consistent with the present findings. Further work that contrasts the association between Extraversion in bonobo- and human-directed interactions is needed to test this possibility.

For Conscientiousness, significant negative associations were found for frequencies of grooming given and received, for which the interpretation is more difficult. Individuals high on Conscientiousness are more gentle and predictable and less manipulative, impulsive, and bullying. As grooming-exchanges serve an important function in bonobo society for the formation and maintenance of social bonds (Vervaecke et al., 2000b, Sakamaki, 2013, Surbeck and Hohmann, 2015, Stevens et al., 2015), Conscientiousness may be negatively related to being more strategic. In humans and chimpanzees, age-related increases in Conscientiousness are reported (King et al., 2008, Mc Crae et al., 2000). In bonobos, age differences were seemingly absent. However, this may reflect the fact that Conscientiousness in bonobos is comprised of only one aspect of that dimension in chimpanzees with the other aspect being relegated to the bonobo Attentiveness dimension (Weiss et al., 2015). As such, these findings do not necessarily imply low levels of comparative validity.

For Agreeableness and Attentiveness there was little support for validity. Both factors showed few associations with behavioral variables, age or sex. In humans and chimpanzees age-related increases have been documented for Agreeableness (King et al., 2008, Mc Crae et al., 2000), which were not present in bonobos. Also, after Bonferroni correction, Agreeableness was not significantly correlated with coded behaviors. Because an Attentiveness factor was not identified in chimpanzees or humans, we were unable to make a priori assumptions about age and sex effects for this dimension. Based on the item loadings, this dimension may reflect how vigilant individuals are to social and non-social cues in their environment. A similar dimension was related to focus during cognitive tasks in brown capuchin monkeys (Morton et al., 2013). Thus, the absence of significant correlations here and elsewhere may reflect shortcomings of the ethogram used in this study, and further development of the ethogram could reveal significant correlations between these dimensions and behaviors.

Developing valid measures of great ape personality is an important step in learning more about the evolutionary bases and functions of individual differences in personality. The present findings suggest that these dimensions derived from ratings are a promising beginning for studies focusing on how personality profiles influence fitness, or how personality variation is related to proximate mechanisms like candidate gene variation, not only in bonobos, but also in their close relatives, the chimpanzees and humans (Staes et al. 2014, Staes et al., 2015, Staes et al., in prep).

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References

ADAMS, M. J., MAJOLO, B., OSTNER, J., SCHULKE, O., DE MARCO, A., THIERRY, B., ENGELHARDT, A., WIDDIG, A., GERALD, M. S. & WEISS, A. 2015. Personality structure and social style in macaques. *Journal of Personality and Social Psychology,* 109**,** 338-53.

ANDERSSON, A., LAIKRE, L. & BERGVALL, U. A. 2014. Two shades of boldness: novel object and anti-predator behavior reflect different personality dimensions in domestic rabbits. *Journal of Ethology***,** 32, 123-136.

BAKER, K. R., LEA, E. G. & MELFI, V. A. 2015. Comparative personality assessment of three captive primate species: Macaca nigra, Macaca sylvanus, and Saimiri sciureus. *International Journal of Primatology***,** 36, 625-646.

BATES, D., MAECHLER, M., BOLKER, B. & WALKER, S. 2015. Package 'lme4' - Linear Mixed-Effects Models using 'Eigen' and S4.

BOESCH, C. & BOESCH-ACHERMAN, H. 2000. *The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution,* Cambridge, Cambridge University Press.

BOESCH, C., HOHMANN, G. & MARCHANT, L. F. 2002. *Behavioural diversity in chimpanzees and bonobos,* Cambridge, Cambridge University Press.

BUIRSKI, P., PLUTCHIK, R. & KELLERMAN, H. 1978. Sex differences, dominance, and personality in the chimpanzee. *Animal Behaviour,* 26**,** 123-129.

CAPITANIO, J. P. 1999. Personality dimensions in adult male rhesus macaques: Prediction of behaviors across time and situation. *American Journal of Primatology,* 47**,** 299-320.

CARERE, C. & EENS, M. 2005. Unravelling animal personalities: how and why individuals consistently differ. *Behaviour* 142**,** 1149-1157.

CARTER, A. J., MARSHALL, H. H., HEINSOHN, R. & COWLISHAW, G. 2012. Evaluating animal personalities: do observer assessments and experimental tests measure the same thing? *Behavioral Ecology and Sociobiology,* 66**,** 153-160.

COSTA, P., TERRACCIANO, A. & MCCRAE, R. R. 2001. Gender differences in personality traits across cultures: Robust and surprising findings. *Journal of Personality and Social Psychology,* 81**,** 322-331.

D'AMOUR, D. E., HOHMANN, G. & FRUTH, B. 2006. Evidence of leopard predation on bonobos (Pan paniscus). *Folia Primatologica,* 77**,** 212-7.

DE VRIES, H., STEVENS, J. M. G. & VERVAECKE, H. 2006. Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour,* 71**,** 585-592.

DI BITETTI, M. S. 2000. The distribution of grooming among female primates: testing hypotheses with the shannon-wiener index. *Behaviour* 137**,** 1517-1540.

DUTTON, D. M. 2008. Subjective assessment of chimpanzee (Pan troglodytes) personality: reliability and stability of trait ratings. *Primates,* 49**,** 253-9.

FRANZ, C. 1999. Allogrooming behavior and grooming site preferences in captive bonobos (Pan paniscus): Association with female dominance. *International Journal of Primatology,* 20**,** 525-546.

FREEMAN, H. D. & GOSLING, S. D. 2010. Personality in nonhuman primates: a review and evaluation of past research. *American Journal of Primatology,* 72**,** 653-71.

FREEMAN, H. D., WEISS, A. & ROSS, S. R. 2016. Atypical early histories predict lower extraversion in captive chimpanzees. *Developmental Psychobiology*, 58, 519-27.

FURUICHI, T. 2011. Female contributions to the peaceful nature of bonobo society. *Evolutionary Anthropology,* 20**,** 131-42.

GARAI, C., WEISS, A., ARNAUD, C. & FURUICHI, T. 2016. Personality in wild bonobos (Pan paniscus). *American Journal of Primatology*, DOI: 10.1002/ajp.22573.

GODIN, J. J. & DUGATKIN, L. A. 1996. Female mating preference for bold males in the guppy, Poecilia reticulata. *Proceedings of the National Academy of Sciences of the United States of America,* 93**,** 10262-10267.

GOLDBERG, L. R. 1990. An alternative "description of personality": the big-five factor structure. *Journal of Personality and Social Psychology,* 59**,** 1216-1229.

GOODALL, J. 1986. *The chimpanzees of Gombe: patterns of behavior. ,* Cambridge, Harverd University Press.

GOSLING, S. D. 1998. Personality Dimensions in Spotted Hyenas (Crocuta crocuta). *Journal of Comparative Psychology,* 112**,** 107-118.

GOSLING, S. D. 2001. From mice to men: What can we learn about personality from animal research? *Psychological Bulletin,* 127**,** 45-86.

GOSLING, S. D. & JOHN, O. P. 1999. Personality dimensions in nonhuman animals: a cross species review. *Current Directions in Psychological Science,* 8**,** 69-75.

GOSLING, S. D. & VAZIRE, S. 2002. Are we barking up the right tree? Evaluating a comparative approach to personality. *Journal of Research in Personality,* 36**,** 607-614.

HARE, B., WOBBER, V., WRANGHAM, R. 2012 The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, 83, 573-585.

HALEKOH, U. & HOJSGAARD, S. 2014. A Kenward-Roger Approximation and Parametric Bootstrap Methods for Tests in Linear Mixed Models – The R Package pbkrtest. *Journal of Statistical Software,* 59**,** 1-32.

HERRMANN, E., HARE, B., CISSEWSKI, J. & TOMASELLO, M. 2011. A comparison of temperament in nonhuman apes and human infants. *Developmental Science,* 14**,** 1393-405.

HOHMANN, G. & FRUTH, B. 2002. Dynamics in social organization of bonobos (Pan paniscus). *In:* BOESCH, C., HOHMANN, G. & MARCHANT, L. F. (eds.) *Behavioral diversity in chimpanzees and bonobos.* Cambridge: Cambridge University Press.

KANO, T. 1992. *The last ape: pygmy chimpanzee behavior and ecology,* Stanford, Stanford University Press.

KING, A. J., FURTBAUER, I., MAMUNEAS, D., JAMES, C. & MANICA, A. 2013. Sex-differences and temporal consistency in stickleback fish boldness. *PLoS One,* 8**,** e81116.

KING, J. E., WEISS, A. & SISCO, M. M. 2008. Aping humans: age and sex effects in chimpanzee (Pan troglodytes) and human (Homo sapiens) personality. *Journal of Comparative Psychology,* 122**,** 418-27.

KONEČNÁ, M., LHOTA, S., WEISS, A., URBANEK, T., ADAMOVA, T. & PLUHACEK, J. 2008. Personality in free-ranging Hanuman langur (Semnopithecus entellus) males: subjective ratings and recorded behavior. *Journal of Comparative Psychology,* 122**,** 379-89.

KUHAR, C. W., STOINSKI, T. S., LUKAS, K. E. & MAPLE, T. L. 2006. Gorilla Behavior Index revisited: Age, housing and behavior. *Applied Animal Behaviour Science,* 96**,** 315-326.

MARTIN, P. R. & BATESON, P. P. G. 1993. *Measuring Behaviour: An Introductory Guide.,* Cambridge, UK, Cambridge University Press.

MASSEN, J., ANTONIDES, A., ARNOLD, A.-M., BIONDA, T. & KOSKI, S. E. 2013. A behavioral view on chimpanzee personality exploration tendency, persistence, boldness and tool-orientation measured with group experiments. *American Journal of Primatology,* 75**,** 947-958.

MC CRAE, R. R., COSTA, J. P. T., HREBICKOVA, M., OSTENDORF, F., ANGLEITNER, A., AVIA, M. D., SANZ, J. & SANCHEZ-BERNARDOS, M. L. 2000. Nature Over nurture: Temperament, personality, and life span development. *Journal of Personality and Social Psychology,* 78**,** 173-186.

MCCRAE, R. R. & COSTA, P. T. 1999. A five-factor theory of personality. *In:* PERVIN, L. & JOHN, O. P. (eds.) *Handbook of Personality* New York: Guilford Press.

MCCRAE, R. R., COSTA, P. T., PEDROSO DE LIMA, M., SIMOES, A., OSTENDORF, F., ANGLEITNER, A., CAPRARA, G. V., BARBARANELLI, C., MARUSIC, I., BRATKO, D. & CHAE, J. 1999. Age differences in personality across the adult life span: Parallels in five cultures. *Developmental Psychology,* 35**,** 466-477.

MEHTA, P. H. & GOSLING, S. D. 2008. Bridging human and animal research: a comparative approach to studies of personality and health. *Brain, Behavior, and Immunity,* 22**,** 651-61.

MORTON, B. F., LEE, P. C., BUCHANAN-SMITH, H. M., BROSNAN, S. F., THIERRY, B., PAUKNER, A., DE WAAL, F. B. M., WIDNESS, J., ESSLER, J. L. & WEISS, A. 2013. Personality structure in brown capuchin monkeys (Sapajus apella): Comparisons with chimpanzees (Pan troglodytes), orangutans (Pongo spp.), and rhesus macaques (Macaca mulatta). *Journal of Comparative Psychology***,** doi: 10.1037/a0031723.

MURRAY, L. 2011. Predicting Primate behavior from Personality Ratings. *In:* WEISS, A., KING, J. E. & MURRAY, L. (eds.) *Personality and Temperament in Non-Humans Primates.* New York: Springer.

NAKAGAWA, S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology* 15**,** 1044-1045.

PAOLI, T. & PALAGI, E. 2009. What does agonistic dominance imply in bonobos? *In:* FURUICHI, T. & THOMPSON, J. (eds.) *The bonobos: Behavior, Ecology and Conservation.* Springer.

PARISH, A. R. 1996. Female relationships in bonobos (Pan paniscus) - Evidence for bonding, cooperation, and female dominance in a male-philopatric species. *Human Nature,* 7**,** 61-69.

PAUNONEN, S.V. 2003. Big five factors of personality and replicated predictions of behavior. *Journal of Personality and Social Psychology*, 84, 411-424

PEDERSON, A. K., KING, J. E. & LANDAU, V. I. 2005. Chimpanzee (Pan troglodytes) personality predicts behavior. *Journal of Research in Personality,* 39**,** 534-549.

PRADO-MARTINEZ, J., SUDMANT, P. H., KIDD, J. M., LI, H., KELLEY, J. L., LORENTE-GALDOS, B., VEERAMAH, K. R., WOERNER, A. E., O'CONNOR, T. D., SANTPERE, G., CAGAN, A., THEUNERT, C., CASALS, F., LAAYOUNI, H., MUNCH, K., HOBOLTH, A., HALAGER, A. E., MALIG, M., HERNANDEZ-RODRIGUEZ, J., HERNANDO-HERRAEZ, I., PRUFER, K., PYBUS, M., JOHNSTONE, L., LACHMANN, M., ALKAN, C., TWIGG, D., PETIT, N., BAKER, C., HORMOZDIARI, F., FERNANDEZ-CALLEJO, M., DABAD, M., WILSON, M. L., STEVISON, L., CAMPRUBI, C., CARVALHO, T., RUIZ-HERRERA, A., VIVES, L., MELE, M., ABELLO, T., KONDOVA, I., BONTROP, R. E., PUSEY, A., LANKESTER, F., KIYANG, J. A., BERGL, R. A., LONSDORF, E., MYERS, S., VENTURA, M., GAGNEUX, P., COMAS, D., SIEGISMUND, H., BLANC, J., AGUEDA-CALPENA, L., GUT, M., FULTON, L., TISHKOFF, S. A., MULLIKIN, J. C., WILSON, R. K., GUT, I. G., GONDER, M. K., RYDER, O. A., HAHN, B. H., NAVARRO, A., AKEY, J. M., BERTRANPETIT, J., REICH, D., MAILUND, T., SCHIERUP, M. H., HVILSOM, C., ANDRES, A. M., WALL, J. D., BUSTAMANTE, C. D., HAMMER, M. F., EICHLER, E. E. & MARQUES-BONET, T. 2013. Great ape genetic diversity and population history. *Nature,* 499**,** 471-475.

RÉALE, D., READER, S. M., SOL, D., MCDOUGALL, P. T. & DINGEMANSE, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological reviews of the Cambridge Philosophical Society,* 82**,** 291-318.

SAKAMAKI, T. 2013. Social grooming among wild bonobos (Pan paniscus) at Wamba in the Luo Scientific Reserve, DR Congo, with special reference to the formation of grooming gatherings. *Primates***,** DOI 10.1007/s10329-013-0354-6.

SCHROEPFER-WALKER, K., HARE, B. & WOBBER, V. 2015. Experimental evidence that grooming and play are social currency in bonobos and chimpanzees. *Behaviour,* 152**,** 545-562.

STAES, N., KOSKI, S. E., HELSEN, P., FRANSEN, E., EENS, M. & STEVENS, J. M. G. 2015. Chimpanzee sociability is associated with vasopressin (Avpr1a) but not oxytocin receptor gene (OXTR) variation. *Hormones and Behavior,* 75**,** 84–90.

STAES, N., STEVENS, J. M. G., HELSEN, P., HILLYER, M., KORODY, M. & EENS, M. 2014. Oxytocin and Vasopressin Receptor Gene Variation as a Proximate Base for Inter- and Intraspecific Behavioral Differences in Bonobos and Chimpanzees. *PLoS One,* 9**,** e113364.

STAES, N., M., EENS, WEISS, A. & STEVENS, J. M. G. Submitted. Combining observational contexts to assess bonobo personality leads to more robust dimensions. *Animal Behaviour*STAES, N., WEISS, A., HELSEN, P., KORODY, M., EENS, M. & STEVENS, J. M. G. In prep. Bonobo personality traits are heritable and associated with vasopressin receptor gene 1a variation.

STEVENS, J. M. G., DE GROOT, E. & STAES, N. 2015. Relationship quality in captive bonobo groups. *Behaviour,* 152**,** 259-283.

STEVENS, J. M. G., VERVAECKE, H., VRIES, H. & ELSACKER, L. 2007. Sex differences in the steepness of dominance hierarchies in captive bonobo groups. *International Journal of Primatology,* 28**,** 1417-1430.

STUMPF, R. M. 2007. Chimpanzees and bonobos: diversity within and between species. *In:* CAMPBELL, C. J., FUENTES, A., MACKINNON, K. C., PANGER, M. & BEARDER, S. K. (eds.) *Primates in Perspective.* Oxford: Oxford University Press.

SURBECK, M. & HOHMANN, G. 2013. Intersexual dominance relationships and the influence of leverage on the outcome of conflicts in wild bonobos (Pan paniscus). *Behavioral Ecology and Sociobiology*, 67, 1767–1780.

SURBECK, M. & HOHMANN, G. 2015. Social preferences influence the short-term exchange of social grooming among male bonobos. *Animal Cognition,* 18**,** 573-9.

UHER, J. & ASENDORPF, J. B. 2008. Personality assessment in the Great Apes: Comparing ecologically valid behavior measures, behavior ratings, and adjective ratings. *Journal of Research in Personality,* 42**,** 821-838.

VAN OERS, K. 2005. Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behavioral Ecology,* 16**,** 716-723.

VAZIRE, S., GOSLING, S. D., DICKEY, A. S. & SHAPIRO, S. J. 2007. Measuring personality in nonhuman animals. *In:* ROBINS, R. W., FRALEY, R. C. & KRUEGER, R. (eds.) *Handbook of Research Methods in Personality Psychology.* New York: Guilford Press.

VERVAECKE, H., DE VRIES, G. J. & VAN ELSACKER, L. 2000a. Dominance and its behavioral measures in a captive group of bonobos (Pan paniscus). *International Journal of Primatology,* 21**,** 47-68.

VERVAECKE, H., DE VRIES, G. J. & VAN ELSACKER, L. 2000b. The pivotal role of rank in grooming and support behavior in a captive group of bonobos (Pan paniscus). *Behaviour* 137**,** 1463-1485.

WEISS, A., ADAMS, M. J., WIDDIG, A. & GERALD, M. S. 2011. Rhesus macaques (Macaca mulatta) as living fossils of hominoid personality and subjective well-being. *Journal of Comparative Psychology,* 125**,** 72-83.

WEISS, A., INOUE-MURAYAMA, M., HONG, K. W., INOUE, E., UDONO, T., OCHIAI, T., MATSUZAWA, T., HIRATA, S. & KING, J. E. 2009. Assessing chimpanzee personality and subjective well-being in Japan. *American Journal of Primatology,* 71**,** 283-92.

WEISS, A., INOUE-MURAYAMA, M., KING, J. E., ADAMS, M. J. & MATSUZAWA, T. 2012. All too human? Chimpanzee and orang-utan personalities are not anthropomorphic projections. *Animal Behaviour,* 83**,** 1355-1365.

WEISS, A. & KING, J. E. 2015. Great ape origins of personality maturation and sex differences: a study of orangutans and chimpanzees. *Journal of Personality and Social Psychology,* 108**,** 648-64.

WEISS, A., KING, J. E. & HOPKINS, W. D. 2007. A cross-setting study of chimpanzee (Pan troglodytes) personality structure and development: zoological parks and Yerkes National Primate Research Center. *American Journal of Primatology,* 69**,** 1264-77.

WEISS, A., STAES, N., PEREBOOM, J. J. M., INOUE-MURAYAMA, M., STEVENS, J. M. G. & EENS, M. 2015. Personality in bonobos. *Psychological Science*, 26**,** 1430-1439.

WOBBER, V., WRANGHAM, R., HARE, B. 2010 Bonobos exhibit delayed development of social behavoir and cognition relative to chimpanzees. *Current Biology*, 20, 226-230.